

The Reproductive System of the British Turridae

(GASTROPODA : TOXOGLOSSA)

BY

EDMUND H. SMITH

Department of Zoology, University of Glasgow, and the Marine Station, Millport¹

(Plate 18; 16 Text figures)

THAT THE NEOGASTROPODS exhibit a similar organization in their reproductive systems has been well illustrated in the families Muricidae, Buccinidae and Nassariidae (FRETTER, 1941; JOHANSSON, 1942, 1957; FRETTER & GRAHAM, 1962). Few species have been described from the families Conidae, Terebridae, Olividae, Columbellidae and Turridae (RISBEC, 1955; MARCUS, 1959, 1960, 1962; ROBINSON, 1960) and the aim of the present paper is to provide a more detailed account of the reproductive system of the Turridae than has been published hitherto. The species examined were *Haedropleura septangularis* (MONTAGU, 1803); *Philbertia leufroyi boothi* (SMITH, 1839); *Cenodagreutes aethus* E. H. SMITH, 1967; *Cenodagreutes coccyginus* E. H. SMITH, 1967; *Mangelia attenuata* (MONTAGU, 1803); *Lora trevelliana* (TURTON, 1834); *Lora turricula* (MONTAGU, 1803). This last species is of particular interest since it exhibits a form of protandric consecutive sexuality which has not been previously recorded in the Prosobranchia.

METHODS

The animals were removed from their shells, relaxed in propylene phenoxetyl (OWEN, 1955) and fixed in Bouin's or Gilson's fluid. The fixed material was sectioned and stained with Alcian blue, haemalum and eosin. Heidenhain's iron haematoxylin and Mallory's triple stains were used for the study of the glandular parts of the reproductive system.

MALE REPRODUCTIVE SYSTEM

In the typical male reproductive system (Figure 1) the testis (t) shares part of the visceral mass with the digestive diverticula (dd) which may even be partly displaced

during the height of the reproductive period. The testicular duct leaves the testis and progresses along the columella muscle to enter the prostate gland (pg) at the posterior end of the mantle cavity. This duct can be divided into the vesicula seminalis which is the portion nearest the testis and the vas deferens (vd) which is the narrow part entering the prostate gland. The vesicula seminalis is dis-

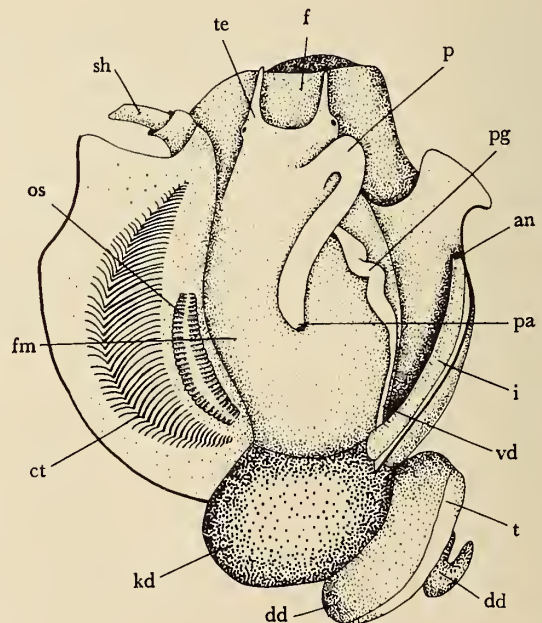


Figure 1

Typical Male System

an - anus	ct - ctenidium	dd - digestive diverticula
f - foot	fm - floor of mantle cavity	i - intestine
kd - kidney	os - osphradium	p - penis
pg - prostate gland	pa - opening of penis	t - testis
sh - siphon	te - tentacles	vd - vas deferens

¹ Present address: Pacific Marine Station, Dillon Beach, California 94929.

tended with sperm during the breeding season and sometimes functions in the ingestion of excess sperm. In some species a gonopericardial duct or a connective tissue remnant of the duct joins the vas deferens with the pericardium. The convoluted prostate gland lies on the left side of the mantle cavity (fm) and in some species incomplete fusion of the two lobes of the gland leaves an opening into the mantle cavity. A duct leads from the prostate to the base of the penis (p) and then continues along the length of the penis to open at its tip. The penis itself lies along the left side of the mantle cavity and in some species actually curves to the right along the posterior limit of the cavity.

Haedropleura septangularis

The thin wall of the long, folded vesicula seminalis of *Haedropleura septangularis* (Figure 2, vs) is composed of

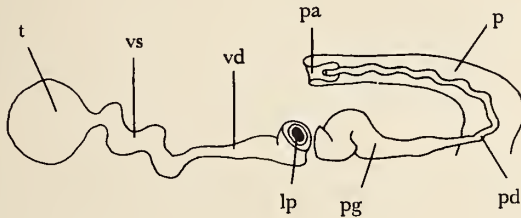


Figure 2

Haedropleura septangularis

Diagrammatic Reconstruction from Sections of the Male System

- lp - lumen of prostate gland
- p - penis
- pa - opening of penis
- pd - duct from prostate
- pg - prostate gland
- t - testis
- vd - vas deferens
- vs - vesicula seminalis

a low epithelium surrounded by connective tissue; no sperm ingestion was found. The vas deferens (vd), as it leaves the vesicula seminalis (vs) is lined by glandular cells which contain small, yellow particles concentrated along their apical borders. No gonopericardial duct nor any remnant of one could be found. After the vas deferens leaves the area of the pericardium it narrows, becomes heavily ciliated, and is surrounded by a thick muscular layer. The long prostate gland (pg) which extends from the area of the kidney, through the ventral floor of the cephalic haemocoel, to the penis (p), is convoluted with an indistinct midventral line of fusion between its two lobes; no opening into the mantle cavity could be found. The ciliated epithelium lining the lumen of the gland (lp) is underlain by a layer of circular muscles and also present are subepithelial gland cells of two types: mucous cells which form the dorsal portion of the gland and clusters of large, darkly staining cells which form the ventral

part. These latter cells contain refractile inclusions throughout their cytoplasm and open into the lumen by long ducts which pass through the circular muscles and between the ciliated cells.

The convoluted duct from the prostate gland (pg) to the tip of the penis (pa) is ciliated and surrounded by a thin, muscular layer. The large penis (p) reaches far into the mantle cavity with its tip turning to the right along the posterior limit. The spermiduct does not open directly at the tip of the penis but into a shallow cavity formed by the inpocketing of the two muscle layers. The penis is covered by a layer of cuticular cells interspaced by scattered mucous cells.

In view of the fact that most of the male turrids studied exhibit a similar pattern in their reproductive systems, the following species will be briefly compared to *Haedropleura septangularis*.

Philbertia leufroyi boothi

In contrast to *Haedropleura septangularis* the vesicula seminalis of *Philbertia leufroyi boothi* (Figure 3, vs) is covered by a thick layer of circular muscle and lined with a glandular epithelium which is engaged in ingesting sperm. The sperm is attached to the apical pole of the

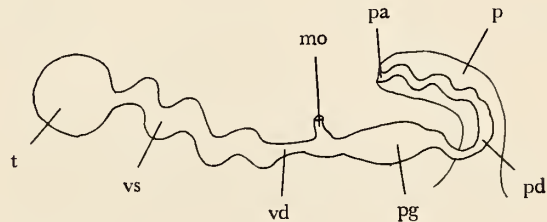


Figure 3

Philbertia leufroyi boothi

Diagrammatic Reconstruction from Sections of the Male System

- mo - opening from vas deferens to mantle
- p - penis
- pa - opening of penis
- pd - duct from prostate
- pg - prostate gland
- t - testis
- vd - vas deferens
- vs - vesicula seminalis

ingesting cells where it is engulfed and deposited in small vacuoles. The epithelium of the vas deferens (vd) is composed of short, ciliated, columnar cells resting on a thick basement membrane and the muscular layer below this membrane is thinner than that surrounding the vesicula seminalis. An opening into the mantle cavity which sometimes occurs when there is incomplete fusion of the lobes of the prostate gland is, in this species, at the end of a short, ciliated duct (mo) from the vas deferens (vd) where the vas deferens joins the prostate gland (pg). The

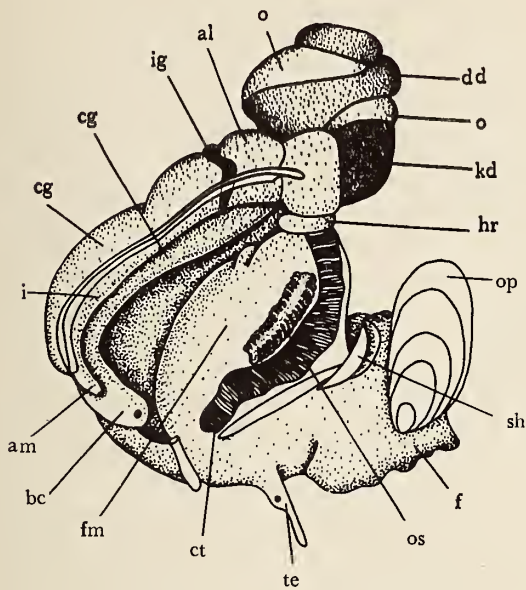


Figure 6

Typical Female System

al - albumen gland	an - anus	bc - bursa copulatrix
cg - capsule gland	ct - ctenidium	dd - digestive diverticula
f - foot	fm - floor of mantle cavity	hr - heart
i - intestine	ig - ingesting gland	kd - kidney
op - operculum	os - osphradium	sh - siphon
	te - tentacles	

a receptaculum seminis and ingesting gland (ig) lie between the albumen gland and capsule gland. A duct connects the receptaculum with the pallial oviduct. The capsule gland is the largest organ of the female system and lies along the left side of the mantle cavity. This gland opens into the bursa copulatrix (bc) which in turn opens into the mantle cavity slightly anterior to the anal opening (an).

Haedropleura septangularis

The gonadial oviduct (Figure 7, go) is composed of columnar gland cells with a lightly staining basal ergastoplasm and is surrounded by a thick muscular layer. No evidence of egg yolk absorption was found (FRETTER, 1941).

The renal oviduct (ro) is short, narrow, and enters the albumen gland (al) ventrally. There is no gonopericardial duct.

The large albumen gland has a ciliated lumen (la) that is partially divided medially by a thin septum (sp) which extends halfway to the floor from its dorsal wall. The entire gland is surrounded by a thick muscular layer. The

anterior end of the gland opens into the capsule gland (cg) through a very short, ciliated pallial oviduct (po).

The large ingesting gland (ig) lies between the albumen (al) and capsule glands (cg) and extends for a short

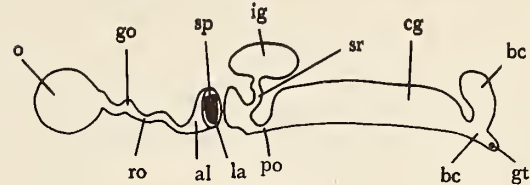


Figure 7

Haedropleura septangularis

Diagrammatic Reconstruction from Sections of the Female System

al - albumen gland	bc - bursa copulatrix	cg - capsule gland
go - gonadial oviduct	gt - genital opening	ig - ingesting gland
la - lumen of albumen gland	o - ovary	po - pallial oviduct
ro - renal oviduct	sp - septum	sr - receptaculum seminis

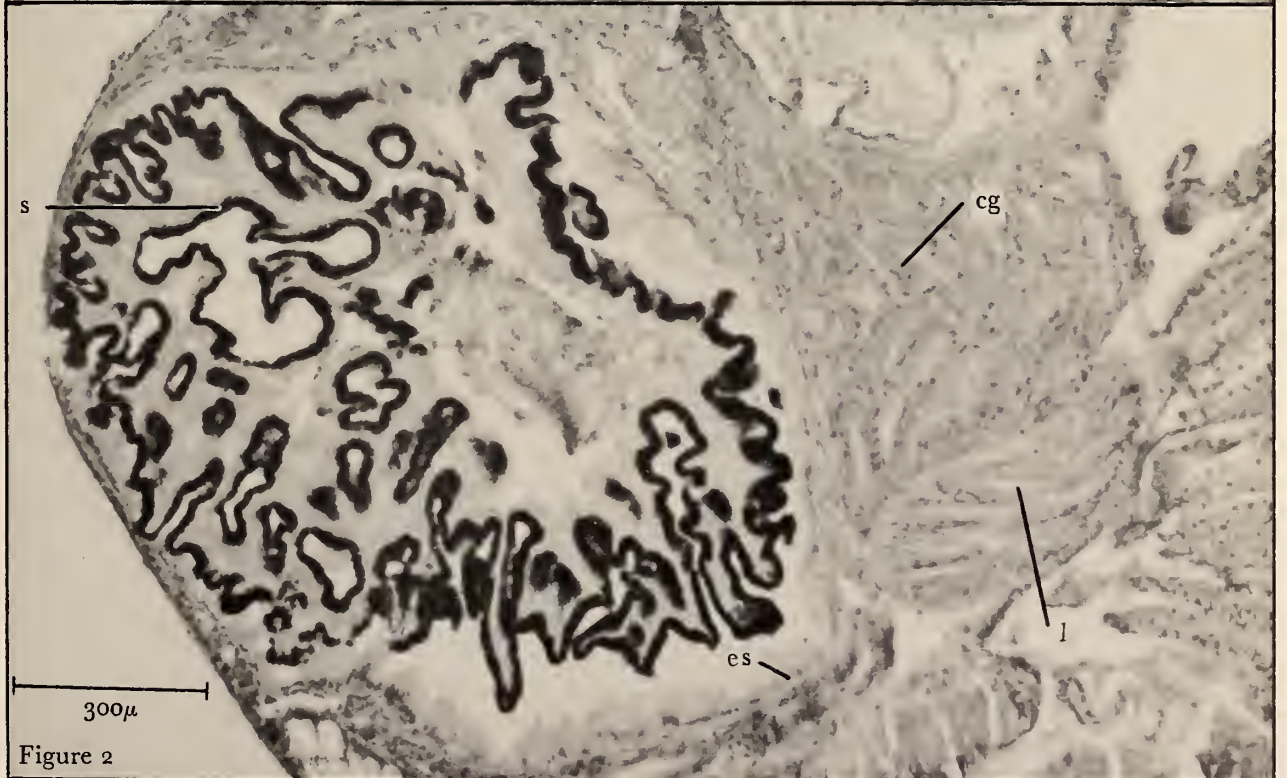
distance over the dorsal surface of the latter. The gland is not attached to the pallial oviduct (po) but to the anterior end of the albumen gland (al) by a long, narrow, ciliated duct which acts as a receptaculum seminis (sr). This fact would indicate that the most likely place for fertilization would be in the albumen gland (al) and not in the pallial oviduct (po). The lumen of the ingesting gland is filled with oriented sperm cells arranged in convoluted rows and not attached to the walls. Some sperm ingestion does occur, but the epithelium is so thin that the amount of sperm ingested, when compared to the vast amount of sperm present in the lumen, must be small.

The capsule gland (cg), although somewhat more complex in its staining properties than those of the muricids and buccinids, is essentially similar in its morphology to that described by FRETTER & GRAHAM (1962) for *Thais lapillus*.

An elongated bursa copulatrix (bc) runs dorsad along the anterior end of the capsule gland (cg) and curves slightly posteriad at the distal end of the capsule gland. The bursa is lined anteriorly by a mucoid epithelium interspaced by small, ciliated cells. Further to the posterior the epithelium changes to a low, ciliated, cuboidal layer. Oriented sperm were attached to this ciliated epithelium, while unoriented sperm, mixed with mucus, filled the distal end of the bursa. The entire bursa copulatrix is covered by a thick layer of muscle.

Philbertia leufroyi boothi

The gonadial oviduct (Figure 8, go) from the ovary to the albumen gland (al) is short and surrounded by a thin





lumen of the capsule gland (lc). The tall epithelium lining the bursa contains ciliated cells with granular inclusions which are actively secreting into the lumen.

In contrast to *Haedropleura septangularis* a short, non-ciliated duct enters the dorsal surface of the bursa (bc) from a large, round "anterior sperm sac" (as) which lies near the anterior end of the capsule gland (cg). This sac is filled with oriented sperm (Plate 18, Figure 2) with their heads pointing towards the walls (es) of the sac but not in actual contact with the epithelium which consists of long, thin cells filled with granules and small vacuoles. No evidence of sperm ingestion could be found. A somewhat similar "sac," termed a "terminal pouch," was described by MARCUS (1960) in *Hastula cinerea*, but, whereas in this species it is situated anterior to the bursa copulatrix, in *Philbertia leufroyi boothi* it lies dorsally between the bursa and the capsule gland.

Cenodagreutes aethus

The gonadal and renal portions (Figure 10, go, ro) of the oviduct are similar to those of *Haedropleura septangularis*. The albumen gland (al) is ciliated throughout, but contrary to the preceding turrids, there are no subepithelial glands. Instead, large mucous cells interspaced with

ticity when stained with haemalum. The cells rest on a thin basement membrane which is in turn surrounded by a layer of connective tissue.

The capsule gland (cg) is similar to that of *Haedropleura septangularis*, although its staining properties are more complex. The bursa copulatrix (bc) is muscular with a narrow lumen which opens directly into the capsule gland as in *Philbertia leufroyi boothi*. The epithelium lining the capsule gland and extending a short way into the bursa is composed of gland cells which stain deeply in haemalum. This glandular epithelium rapidly gives way to a simple cuboidal layer of cells surrounded by thick (30μ to 60μ), circular muscles.

Cenodagreutes coccyginus

The female system of *Cenodagreutes coccyginus* is very similar to that of *C. aethus*, with some exceptions (Figure 11). There is a pallial oviduct (po) between the albumen gland and the capsule gland (cg).

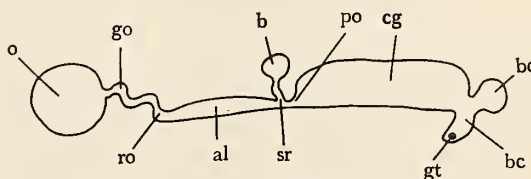


Figure 11

Cenodagreutes coccyginus

Diagrammatic Reconstruction from Sections of the Female System
 al - albumen gland b - bulb bc - bursa copulatrix
 cg - capsule gland go - gonadal oviduct gt - genital opening
 o - ovary po - pallial oviduct ro - renal oviduct
 sr - receptaculum seminis

No sperm were found in the small distal bulb of the receptaculum seminis (sr), nor was there any evidence of sperm ingestion. However, the possibility of sperm ingestion cannot be completely ruled out. The low epithelium lining the terminal bulb of the receptaculum seminis is composed of eosinophilic cells with irregularly shaped granules throughout the cytoplasm. The general histological and morphological data indicate that both bulb and duct function as a receptaculum seminis.

The bursa copulatrix (bc) is much larger than that of *Cenodagreutes aethus* with the bulb forming the distal end of the bursa and lying at the anterior end of the capsule gland (cg). The bulb, although it has become part of the bursa and functions in a different manner, lies in the same position as the "anterior sperm sac" of *Philbertia leufroyi boothi*. It is not lined by glandular epithelium, but by one composed of densely ciliated, cuboidal cells which rest on a thin layer of circular muscle.

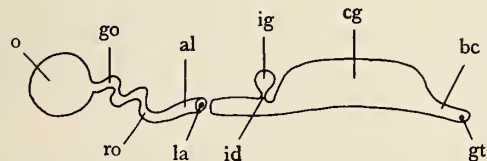


Figure 10

Cenodagreutes aethus

Diagrammatic Reconstruction from Sections of the Female System
 al - albumen gland bc - bursa copulatrix cg - capsule gland
 go - gonadal oviduct gt - genital opening ig - ingesting gland
 id - duct to ingesting gland la - lumen of albumen gland
 o - ovary ro - renal oviduct

ciliated cells form the dorsal wall of the gland while the much thinner ventral wall has only scattered mucous cells. The epithelium of the albumen gland (al) becomes continuous with the posterior part of the capsule gland (cg); a slight constriction rather than a duct marks the boundary between the two glands. Therefore, the pallial oviduct is absent.

A short, constricted, muscular duct joins the anterodorsal part of the albumen gland with the ingesting gland (ig) and functions as a receptaculum seminis (sr). The lumen of the ingesting gland is lined with gland cells possessing large, polymorphic nuclei that exhibit chroma-

Mangelia attenuata

The gonadial oviduct (Figure 12, go) is comprised of tall, glandular cells which are, for the most part, chromatophobic and in which there is a concentration of granules near the apical pole that stains with Alcian blue. In

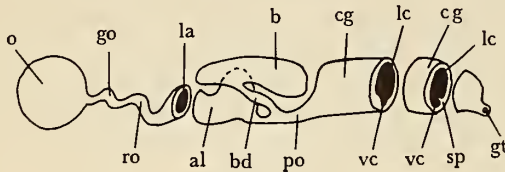


Figure 12

Mangelia attenuata

Diagrammatic Reconstruction from Sections of the Female System

al - albumen gland	b - bulb	bd - duct to bulb
cg - capsule gland	go - gonadial oviduct	gt - genital opening
la - lumen of albumen gland	lc - lumen of capsule gland	o - ovary
o - ovary	po - pallial oviduct	ro - renal oviduct
sp - septum	vc - ventral channel	

contrast to the previously described turrids, a strong sphincter divides the renal oviduct (ro) from the albumen gland (al). This is ciliated throughout and as in both species of *Cenodagreutes* there are no subepithelial glands. The entire gland and the long pallial oviduct (po) connecting it with the capsule gland (cg) are covered by a thick sheet of muscle. The duct is lined by columnar cells bearing dense cilia.

Branching from the pallial oviduct is a long, muscular duct (bd) with a densely ciliated lumen similar to that of the pallial oviduct. This straight duct leads to a very large, elongated bulb (b) which lies over the dorsal surface of the albumen gland and is not branched as in *Mangelia brachystoma* (ROBINSON, 1960). The cells lining the bulb exhibit different stages of intracellular elaboration, culminating in the extrusion of a voluminous globule and they resemble the ingesting type of cell found in *Philbertia leufroyi boothi* in having large, polymorphic nuclei, although neither the duct nor the bulb contained sperm in any of the specimens sectioned and the nature of the epithelium does not suggest an ingesting function.

The capsule gland shows the same staining complexity found in both species of *Cenodagreutes*. As in *Mangelia brachystoma* (ROBINSON, 1960) no separate bursa copulatrix (bc) is present, but a large, ventral channel (vc), which is separated from the capsule gland by a septum (sp), extends posteriorly past the gonopore (gt) for some distance. The penis is inserted into this channel instead of a separate chamber as in the preceding turrids. The septum, which separates the anterior part of the ventral

channel from the capsule gland, disappears posteriorly so that the channel is marked only by a slight constriction.

Lora trevelliana

Whereas in most of the turrids studied the gonadial oviduct (Figure 13, go) is long, in this species it is short and ciliated and, in addition, the cells have a vacuolated cytoplasm with small granules concentrated around the cell walls. The long albumen gland is similar to that of both species of *Cenodagreutes* with some slight staining differences; the gland cells are not subepithelial. The elongated ingesting gland (ig) extends posteriorly over the dorsal surface of the albumen gland (al) and the cells lining the duct to the ingesting gland are densely ciliated,

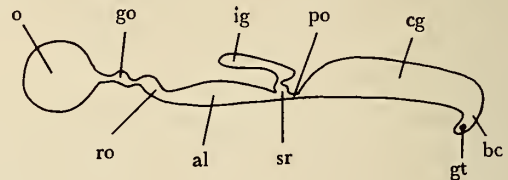


Figure 13

Lora trevelliana

Diagrammatic Reconstruction from Sections of the Female System

al - albumen gland	bc - bursa copulatrix	cg - capsule gland
go - gonadial oviduct	gt - genital opening	ig - ingesting gland
o - ovary	po - pallial oviduct	ro - renal oviduct
	sr - receptaculum seminis	

while the epithelium lining the gland itself is composed of large gland cells actively engaged in sperm ingestion. Oriented sperm cells were found attached to the walls of the duct to the ingesting gland, showing that the duct functions as a receptaculum seminis (sr).

The capsule gland resembles that of *Philbertia leufroyi boothi* in the complexity of its staining reactions. The bursa copulatrix (bc) is an incapacious, elongated structure with an epithelium comprising scattered mucous cells, ciliated cells and large gland cells.

HERMAPHRODITIC SYSTEM

Lora turricula

In a number of specimens of this species both male and female systems were present in the same individual. It was thought best to deal with both the male and the female systems at the same time in order to facilitate discussion of the hermaphroditic condition.

The male system is quite normal and follows a pattern similar to that described for *Lora trevelliana* (Figure 14). The testis (t) shows no evidence of sexual transformation such as the presence of oocytes around the periphery, as found in *Crepidula fornicata* (COE, 1942). The vesicula

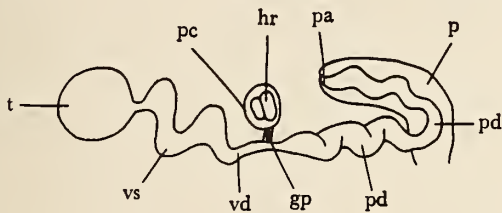


Figure 14
Lora turricula

Diagrammatic Reconstruction from Sections of the Male System

- gp - connective tissue remnant of gonopericardial duct
- hr - heart
- pc - pericardial wall
- vd - vas deferens
- p - penis
- pa - opening of penis
- pd - duct from prostate
- t - testis
- vs - vesicula seminalis

seminalis (vs) is well developed and as in *Philbertia leufroyi boothi*, it is not ciliated but composed of gland cells, which are engaged in sperm ingestion near the testis. These cells rest on a basement membrane which is surrounded by a thin layer of connective tissue. The vas deferens (vd) is convoluted and made up of densely ciliated, cuboidal cells resting upon a thin basement membrane covered by a thin layer of muscle. There is a remnant of the gonopericardial duct (gp) attaching the vas deferens (vd) to the wall of the pericardium (pc).

There is no prostate gland nor opening into the mantle cavity. The ciliated epithelium of the vas deferens changes abruptly, near the posterior end of the kidney, to a mucoid epithelium containing small, ciliated cells wedged between large mucous cells. This type of glandular spermiduct (pd) continues to the tip of the penis as in *Lora trevelliana*.

A number of predominantly female specimens had large, round penes (Figure 15). In these specimens there was no trace of testis and only a small portion of the ovary (o) contained oocytes. The remainder of the last two visceral whorls was filled with mature, normal eggs. No evidence of a renal oviduct nor of a gonopericardial duct could be found. The thin gonadial oviduct (go) enters the albumen gland (al) directly, with no sphincter between it and the gland. It is composed of a non-glandular epithelium surrounded by a thin muscular layer.

The albumen gland (al) is ciliated and possesses sub-epithelial cells which are of two kinds. Those of the dorsal wall color deeply with Alcian blue, while those of the ventral wall stain with haemalum. The albumen gland opens into the capsule gland (cg) through a short, ciliated pallial oviduct (po); a thin layer of muscle surrounds the duct.

The ciliated ventral channel leads posteriorly from the bursa copulatrix (bc) along the ventral part of the capsule gland (cg) to join the pallial oviduct (po).

A short, ciliated duct connects the elongated receptaculum seminis (sr) to the pallial oviduct (po). The bulb is lined with a very thin (1.3μ), non-glandular epithelium. No evidence of sperm ingestion could be found, and indeed the thin epithelium does not seem to be of the type capable of ingesting sperm. The duct and receptaculum seminis are surrounded by a thin (4μ) muscle layer.

The well developed capsule gland (cg) is similar to that of *Lora trevelliana*, except that the three histological areas present in other species react differently to the same stain. The bursa copulatrix (bc) is very muscular with a large, ciliated lumen; gland cells are absent.

The male system, which is present in these same female specimens, consists of a normal penis (p) and glandular spermiduct (pd), which terminates in a sperm filled bulb near the albumen gland (al) of the female. Unoriented sperm was found along the spermiduct almost as far as the penis tip (pa).

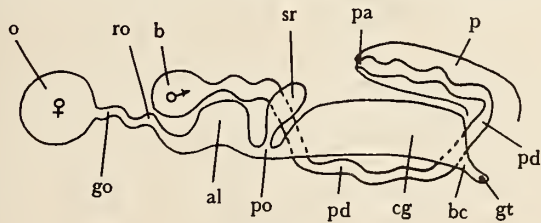


Figure 15

Diagrammatic Reconstruction from Sections of the Female System with the nearly complete Male System

- al - albumen gland
- bc - bursa copulatrix
- cg - capsule gland
- go - gonadial oviduct
- o - ovary
- pd - duct from prostate
- po - pallial oviduct
- sr - receptaculum seminis
- b - bulb
- gt - genital opening
- p - penis
- pa - opening of penis
- ro - renal oviduct

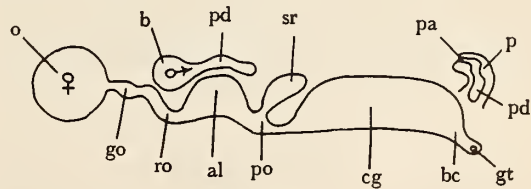


Figure 16

Diagrammatic Reconstruction from Sections of the Female System with Vestiges of the Male System

- al - albumen gland
- bc - bursa copulatrix
- cg - capsule gland
- go - gonadial oviduct
- o - ovary
- pd - duct from prostate
- po - pallial oviduct
- sr - receptaculum seminis
- b - bulb
- gt - genital opening
- p - penis
- pa - opening of penis
- ro - renal oviduct

In one of the female specimens (Figure 16) the male system had atrophied so that only the terminal bulb (b), near the albumen gland (al) of the female, and a short portion of the glandular spermiduct remained. The penis was very reduced with no sperm present in any part of the male system.

PEDAL GLANDS

Within the neogastropods the pedal glands are not entirely engaged in lubricating the foot during locomotion. They may undertake such diverse functions as moulding and attaching egg capsules or aiding in the boring of holes in the shell or hard exoskeleton of the prey.

The anterior pedal mucous glands open into a ciliated, sagittal canal in the turrids studied. In many cases these subepithelial glands do not react with Alcian blue nor give any indication of the presence of an acid mucopolysaccharide. In *Philbertia leufroyi* and *Mangelia attenuata* scattered mucous clusters occur mixed with darker, blue staining cells on both sides of the sagittal canal. In *Cenodagreutes aethus* and *C. coccyginus* the anterior pedal glands give three staining reactions. Some gland clusters stain with haemalum, some with eosin and haemalum, and a few others with Alcian blue.

"Sole glands" is a collective term applied by FRETTER & GRAHAM (1962) to include all the glands which pour secretions onto the surface of the sole, including goblet cells, which lie within the epithelium and subepithelial glands. In *Philbertia leufroyi boothi* a large mass of subepithelial glands fills much of the mesopodium. The gland cell clusters stain intensely with Alcian blue and open between the ciliated epithelial cells by long ducts onto the surface of the foot. In *Mangelia attenuata* the epithelium covering the sole is composed of eosinophilic cells interspaced by ciliated cells, mucous cells and subepithelial glands being absent. The posterior pedal mucous gland, which occurs in some rissoids and triphorids, is absent. The ventral pedal gland present in female muricids and buccinids and concerned with the final moulding and attachment of the egg capsules, is totally absent.

DISCUSSION

The neogastropod reproductive system has been considered uniformly dioecious and it is, therefore, surprising to find that *Lora turricula* exhibits a form of hermaphroditism. In the mesogastropod genera, which exhibit true protandric consecutive sexuality, such as *Calyptrea*, *Crepidula* and *Crucibulum*, each individual functions as one sex when young (male) and as the opposite sex when

older. The histological basis of this type of sexuality depends upon the presence of an ambisexual gonad (COE, 1944). In addition, the male genital system is reconstructed into an oviduct, seminal receptaculum and vagina during the transition from the male phase to the female phase. This is not the case with *L. turricula*, since there is no ambisexual gonad, and the male and female reproductive systems are found together in the same individual. In *L. turricula* the gonads undergo a similar cycle to that described by YONGE (1962) for *Trichotropis cancellata*, where the gonads are undifferentiated during the transition from the male to the female phase. However, *L. turricula* differs from the above gastropods and from *T. borealis* (GRAHAM, 1956) in having two separate and complete reproductive systems present in the same individual, although the male system is no longer connected to the gonads and gradually atrophies during the change to the female phase, eventually leaving a separate, functional female system. This type of hermaphroditism is similar to that found in the pulmonates and opisthobranchs except that both sexual systems are not complete at the same time. It is conceivable that some specimens of *L. turricula* could act as functional hermaphrodites during the brief transitional phase when there is still sperm in the male duct and a well developed penis still present. The possibility of self-fertilization, as suggested by YONGE (1962) for *T. cancellata*, where the penis remains throughout the life of the female, seems remote in *L. turricula*.

In *Patella vulgata*, which exhibits alternative sexuality, ORTON, SOUTHWARD & DODD (1956) found, in a single population, that 90% of the small specimens, 16 - 25 mm in shell length, were males. Those with shells 40 mm long were male and female in equal numbers, while 60 - 70% of the larger animals, with shells 60 mm in length or longer, were female. Earlier ORTON (1919, 1928) suggested that the young population contained two kinds of male-phase individuals, true males and temporary males (protandric females). Due to the difficulty of locating *Lora turricula*, only a small number could be collected. This sample consisted of 15 individuals with an average shell length of 14.8 mm (Table 1). The sample can be broken into 3 males, 5 females, and 7 in various stages of the transitional phase. Contrary to what ORTON found, this small sample can not be broken into distinct sex phases based on shell size. The results from this sample seem to indicate that the population may consist of two sexual phases: a pure male phase and a temporary male phase (protandric hermaphrodite), later becoming female.

Populations of *Lora turricula* are probably restricted to small geographic areas by a number of complex factors, including specialized feeding habits and particle size of the substrate. Therefore, this form of hermaphroditism would be of direct importance to such insular populations

Table 1

Occurrence and Condition of the Reproductive Systems
in 15 Specimens of *Lora turricula* Collected from the
Clyde Sea Area, Scotland, During June, 1964.

No.	Shell size mm	Sex	Condition of reproductive system
1	9.7	♂	well developed male and female systems
2	12.5	♂	typical male, no trace of female system
3	13.0	♂	very reduced penis present
4	13.0	♀	well developed male and female systems, no testis present
5	13.5	♀	well developed female, no male system present
6	14.0	♀	well developed female, no male system present
7	14.5	♂	typical male, no trace of female system
8	14.5	♂	very reduced penis present
9	15.3	♂	typical male, no trace of female system
10	16.0	♀	well developed female, no male system present
11	16.6	♀	well developed male and female systems, no testis present
12	16.7	♀	very reduced penis present
13	17.3	♀	well developed female, no male system present
14	17.5	♀	well developed female, no male system present
15	18.8	♀	well developed male and female systems, no testis present

by assuring the presence of both males and females. Two causal factors have been indicated in the evolution of the hermaphroditic state, genetic change and environmental conditions (FRETTER & GRAHAM, 1964). Obviously, a genetic change has taken place in the isolated population studied and evidently hermaphroditism has not been selected against by the environmental conditions. Of course, a number of widely separated populations will have to be sampled in order to show that all populations of *L. turricula* exhibit hermaphroditism.

In some *Stenoglossa* FRETTER (1941) found that sperm ingestion, and in some species egg yolk ingestion, takes place in an ingesting gland located between the albumen and the capsule glands. The convoluted duct, which runs from the ingesting gland to the pallial oviduct, acts as a receptaculum seminis with oriented sperm attached along its walls. JOHANNSON (1957), from his work with *Nassarius pygmaea* and *N. incrassatus*, doubted that sperm ingestion occurred in all *Stenoglossa* which possess a gland in this same position. He also stated that it was not possible to rule out sperm ingestion in these species because of the simplicity of the epithelium lining the gland or because, at the time of sectioning, the gland cells did not contain ingested sperm. Sperm ingestion was not found in the turrid species *Mangelia attenuata* and *Lora trevelliiana*. The histological nature of the epithelium and the condition of the sperm within the gland indicate that it is used for sperm storage as is the duct leading to the gland. This

case agrees with JOHANNSON'S observations with both the gland and duct functioning as a receptaculum seminis.

In the turrids the ingesting gland and the receptaculum seminis are located in a proximal position which at first suggests a homology with the receptaculum of other gastropods, as postulated by FRETTER (1941) for the *Stenoglossa*. However, JOHANNSON (1957) has suggested that the ingesting gland corresponds to a proximal or inner bursa copulatrix and not a receptaculum. Although the turrids studied do not offer exception to FRETTER'S theory, it would be misleading not to mention *Drupa nodulosa* (E. H. SMITH, in preparation) which supports JOHANNSON'S theory since there is in this species both an ingesting gland and a separate receptaculum seminis. In addition, MARCUS (1962) has found that in some species of Columbellidae the pericardial cavity acts as a receptaculum seminis with no sperm ingestion, while in other species the long duct from the pallial oviduct may act as a receptaculum seminis or in some cases as an ingesting gland. From this information on the Columbellidae, it is apparent that the position of the ingesting gland varies in different families of the neogastropods and it is impossible to postulate a general homology for the gland that applies to the whole group.

In some *Stenoglossa* and *Toxoglossa* an "anterior sperm sac" is found. This bulb lies dorsally above the bursa copulatrix and opens into it through a duct or muscular opening. It occurs in the turrid *Philbertia leufroyi boothi*,